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Revisionary Notes on Neotropical Porcupines (Rodentia: Erethizontidae) 3. An Annotated Checklist of the Species of *Coendou* Lacépède, 1799

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ABSTRACT

The erethizontid rodent genus *Coendou* (including *Echinoprocta* and *Sphiggurus*) contains 13 valid species that live in tropical and subtropical forests from Mexico to Uruguay. This report tabulates information about the type material of all Recent nominal taxa referred to the genus, provides synonymies of all species recognized as valid, describes geographic distributions based on examined specimens, cites published descriptions of external and craniodental morphology, summarizes information that supports recommended binomial usage, and suggests where future taxonomic research is likely to be productive. Among other novel results, the nominal taxa *richardsoni* J.A. Allen, 1913, and *rothschildi* Thomas, 1902, are synonymized with *C. quichua* Thomas, 1899; a Paraguayan neotype is designated for *C. spinosus* (F. Cuvier, 1823); and a specimen of *C. rufescens* is reported from Bolivia, extending the range of that species by 1800 km. Additionally, morphometric data are tabulated for several species not treated in previous reports of this series, including *C. bicolor, C. mexicanus, C. prehensilis, C. quichua, C. rufescens,* and *C. spinosus.*

INTRODUCTION

The caviomorph rodent family Erethizontidae includes the familiar North American porcupine (*Erethizon dorsatum*), the Brazilian thin-spined porcupine (*Chaetomys subspinosus*), and

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a series of prehensile-tailed Central and South American species that are among the most taxonomically neglected of New World mammals. Previous reports in this series (Voss and Angermann, 1997; Voss and da Silva, 2001) were intended as early installments of a comprehensive revision of Neotropical erethizontids, but that work has been delayed by other projects and is now unlikely to be completed anytime soon. In the meantime, the absence of an authoritative taxonomic reference is a significant research impediment: molecular sequence data have appeared in the literature with erroneous species identifications, investigators without access to synoptic collections are unable to assess the significance of newly obtained material, and the current taxonomy (Woods and Kilpatrick, 2005) still reflects nomenclatural blunders dating from the middle of the last century. Hence this checklist, annotated as necessary to explain recommended binomial usage for species of *Coendou* (including *Echinoprocta* and *Sphiggurus*).

Thirty-seven nominal taxa representing at least 13 valid Recent species are here referred to *Coendou* (table 1). I have examined the type material of most named forms, but other important specimens that I have not seen are widely scattered among museums on three continents. Additionally, there are still several parts of South America (notably including the Pacific coast of Colombia and much of western Amazonia) from which little or no material is available, and only a few large series exist to document patterns of nongeographic infraspecific variation (an important topic that remains inadequately treated in the literature). Lastly, molecular and karyotypic data, which have proven so helpful in sorting out the taxonomy of other mammalian clades, have yet to be obtained from more than a handful of erethizontid specimens. Inevitably, many aspects of porcupine taxonomy remain obscure.

The species limits and synonymies recognized below are, therefore, intended as hypotheses to be tested by subsequent researchers with access to additional specimens and new data. Because this is a checklist and not a full-scale revision, I omit many elements of the latter, including detailed morphological descriptions, illustrations, range maps, and gazetteers. However, I provide citations to published descriptions, include tabular summaries of measurement data, and list examined specimens to facilitate the identification of species not treated in previous reports of this series. Synonymies for each species recognized as valid include only original descriptions, subsequent novel name combinations, and misspellings; they are not intended as exhaustive catalogs of binomina historically applied to taxa, nor have I been diligent about searching the literature for esoteric variant spellings or eccentric usage.

MATERIALS AND METHODS

Specimens: Specimens that I examined and others referred to in the text are in the American Museum of Natural History, New York (AMNH); the Academy of Natural Sciences, Philadelphia (ANSP); the Natural History Museum, London (BMNH); the Carnegie Museum, Pittsburgh (CM); the Departamento de Biología de la Escuela Politécnica Nacional, Quito (EPN); the Field Museum, Chicago (FMNH); the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); the University of Kansas Biodiversity Research Center, Lawrence (KU); the Los Angeles County Museum, Los Angeles (LACM); the Louisiana State University Museum of

TABLE 1. Type Material and Status of Nominal Taxa Referred to *Coendou*[a]

	Type material	Status (if not valid)	Type(s) examined?
affinis Brandt, 1835	ZINRAS 31[b]	synonym of *C. spinosus*	yes
***bicolor* Tschudi, 1844**	MHNN 94.243A[b]		no
boliviensis Gray, 1850	BMNH 47.11.22.6[b]	synonym of *C. prehensilis*	yes
brandtii Jentink, 1879	RMNH 19642[c]	synonym of *C. prehensilis*	no
centralis Thomas, 1904	BMNH 3.7.7.102[d]	synonym of *C. prehensilis*	yes
couiy Desmarest, 1822	none[e]	nomen oblitum	
cuandu Desmarest, 1818	none[e]	synonym of *C. prehensilis*	
***ichillus* Voss & da Silva, 2001**	AMNH 126171[d]		yes
***insidiosus* Olfers, 1818**	ZMB 1298[b]		yes
koopmani Handley & Pine, 1992	USNM 519689[d]	synonym of *C. nycthemera*	yes
laenatus Thomas, 1903	BMNH 3.3.3.94[d]	synonym of *C. mexicanus*	yes
liebmani Reinhardt, 1844	ZMUC 518, 519[f]	synonym of *C. mexicanus*	no
longicaudatus Daudin, 1802	none[e]	synonym of *C. prehensilis*	
melanurus Gray, 1842	[BMNH] "86a"	synonym of *C. melanurus* Wagner	yes
***melanurus* Wagner, 1842**	NMW 42010[c]		yes
***mexicanus* Kerr, 1792**	none[e]		
nigricans Brandt, 1835	ZINRAS 30[b]	synonym of *C. spinosus*	yes
***nycthemera* Olfers, 1818**	ZMB 1299[b]		yes
pallidus Waterhouse, 1848	BMNH 46.1.9.14[c]	synonym of *C. insidiosus*	yes
platycentrotus Brandt, 1835	ZINRAS 35[b]	synonym of *C. prehensilis*	yes
***prehensilis* Linnaeus, 1758**	MNRJ 73383[g]		no
***pruinosus* Thomas, 1905**	BMNH 5.7.5.9[d]		yes
***quichua* Thomas, 1899**	BMNH 99.2.18.17[d]		yes
richardsoni J.A. Allen, 1913	AMNH 33242[d]	synonym of *C. quichua*	yes
roberti Thomas, 1902	BMNH 3.7.1.97[d]	synonym of *C. spinosus*	yes
***roosmalenorum* Voss & da Silva, 2001**	INPA 2586[d]		yes
rothschildi Thomas, 1902	BMNH 3.3.1.93[d]	synonym of *C. quichua*	yes
***rufescens* Gray, 1865**	BMNH 53.9.28.30[b]		yes
sanctaemartae J.A. Allen, 1904	AMNH 15460[d]	synonym of *C. prehensilis*	yes
sericeus Cope, 1889	ANSP 4804[b]	synonym of *C. spinosus*	yes
simonsi Thomas, 1902	BMNH 2.1.1.103[d]	synonym of *C. bicolor*	yes
sneiderni Lönnberg, 1937	NRM 631263[b]	synonym of *C. rufescens*	no
***spinosus* F. Cuvier, 1823**	USNM 115122[g]		yes
tricolor Gray, 1850	BMNH 46.8.7.9[b]	synonym of *C. prehensilis*	yes
villosus F. Cuvier, 1823	none[h]	synonym of *C. spinosus*	yes
***vestitus* Thomas, 1899**	BMNH 54.6.26.1[d]		yes
yucataniae Thomas, 1902	BMNH 91.3.24.1[d]	synonym of *C. mexicanus*	yes

[a] Only available names based on Recent material are listed. Names of species recognized as valid in this report are in boldface. The gender of epithets originally combined with *Hystrix* (feminine) has been changed to agree with *Coendou* (masculine).

[b] Holotype by monotypy.

[c] Lectotype.

[d] Holotype by original designation.

[e] Based on bibliographic source(s)

[f] Syntypes.

[g] Neotype.

[h] Lost (see text).

Zoology (LSUMZ); the Museum of Comparative Zoology at Harvard University, Cambridge (MCZ); the Muséum d'Histoire Naturelle, Neuchâtel (MHNN); the Muséum National d'Histoire Naturelle, Paris (MNHN); the Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); the Museum of Southwestern Biology at the University of New Mexico, Albuquerque (MSB); the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM); the Museum of Vertebrate Zoology at the University of California, Berkeley (MVZ); the Naturhistoriska Riksmuseet, Stockholm (NRM); the Naturhistorisches Museum Wien, Vienna (NMW); the Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman (OMNH); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); the Royal Ontario Museum, Toronto (ROM); the University of Michigan Museum of Zoology, Ann Arbor (UMMZ); the National Museum of Natural History, Washington (USNM); the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZINRAS); the Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB); and the Zoological Museum of the University of Copenhagen, Copenhagen (ZMUC).

MEASUREMENTS: I recorded external measurements (in millimeters, mm) from collectors' labels, including total length (TL) or head-and-body length (HBL), length of tail (LT), and length of hind foot (HF). For specimens prepared by American collectors (who measure total length), I obtained head-and-body length by subtracting LT from TL. In the absence of collectors' measurements, I obtained approximate values (prefixed by "ca.") for HBL and LT by measuring dried skins to the nearest 5 mm with a flexible rule. Length of the hind foot (HF) includes the claws and was either measured by American collectors in the field (British collectors measure the hind foot without the claws) or remeasured by me on dried skins; only minimally distorted dried hind feet containing the intact pedal skeleton were remeasured. Measurements of the skull and dentition, taken with digital calipers and recorded to the nearest 0.1 mm, are abbreviated and defined as follows (see Voss and Angermann [1997: fig. 4] and Voss and da Silva [2001: fig. 2] for illustrations of measurement endpoints).

CIL	Condylo-incisive length: Measured from the articular surface of one occipital condyle to the greater curvature of the ipsilateral upper incisor
LD	Length of diastema: Measured from the lesser curvature of an upper incisor at the alveolar margin to the crown of the ipsilateral P4
MTR	Maxillary tooth row: Greatest crown length from P4 to M3
LM	Length of molars: Greatest crown length of the upper molar series (M1–M3)
BP4	Breadth of P4: Greatest crown breadth of the permanent upper premolar
BM1	Breadth of M1: Greatest crown breadth of the first upper molar
APB	Anterior palatal breadth: Measured between the crowns of the first upper molars
PPB	Posterior palatal breadth: Measured between the crowns of the third upper molars
PZB	Posterior zygomatic breadth: Greatest breadth across the zygomatic arches behind the orbits
HIF	Height of the infraorbital foramen: Measured as the greatest inside diameter, usually at an angle of about 30°–40° from the midsagittal plane
ZL	Zygomatic length: Measured from the posterior margin of the infraorbital foramen to the posterolateral corner of the zygomatic arch

LN	Length of nasals: Greatest length of one nasal bone (the longest if right and left elements are unequal)
BNA	Breadth of nasal aperture: Greatest transverse dimension of the nasal orifice, always at or near the nasal/premaxillary sutures
BB	Breadth of braincase: Transverse dimension of the braincase, measured by placing the caliper jaws just above the squamosal zygomatic root on each side
DI	Depth of incisor: Distance between the greater and lesser curvatures of an upper tooth
BIT	Breadth of the incisor tips: Measured across the enameled tips of both upper teeth

AGE CLASSIFICATION: I used maxillary tooth eruption, cranial suture closure, and pelage maturation to define a heuristic age classification as follows (after Voss and Angermann, 1997). *Juveniles*: Maxillary tooth row incomplete (three or fewer teeth erupted); all cranial sutures open; pelage often conspicuously immature, including long fur even in species that lack visible fur as adults. *Subadults*: Immature maxillary dentition (dP4–M3) completely erupted, or dP4 shed and P4 incompletely erupted; all cranial sutures still visible; pelage always appears mature. *Adults*: Permanent maxillary dentition (P4–M3) fully erupted, with light to moderate wear (teeth not worn below widest part of crown, usually with at least some occlusal detail remaining); some cranial sutures usually obliterated. *Old adults*: Cheek teeth worn below widest part of crown (and therefore not measurable), with little or no occlusal detail remaining on M1 and M2; few (if any) cranial sutures visible.

Because erroneous taxonomic inferences can result from investigator inability to distinguish subadult from adult specimens, some remarks on the morphology of dP4 and P4 are appropriate. Although these teeth cannot (in my experience) be distinguished unambiguously by occlusal features, dP4 is usually narrower than M1, exhibits more or less the same degree of wear as that tooth, and has widely divergent labial and lingual roots. By contrast, P4 is usually wider than M1, is always less worn than that tooth, and has less divergent roots than its deciduous precursor.

SYSTEMATIC ACCOUNTS

Coendou Lacépède, 1799

Coendou Lacépède, 1799: 11; type species *Hystrix prehensilis* Linnaeus, 1758, by monotypy.
Coendus: E. Geoffroy St.-Hilaire, 1803: 157 (misspelling of *Coendou* Lacépède, 1799).
Coandu: G. Fischer, 1814: 102 (misspelling of *Coendou* Lacépède, 1799).
Sinethere F. Cuvier, 1823: 427; type species *S. prehensilis* (Linnaeus, 1758) by original designation.
Sphiggure F. Cuvier, 1823: 427; type species *S. spinosa* F. Cuvier, 1823, by original designation.
Sinoetherus: F. Cuvier, 1825: 256 (misspelling of *Sinethere* F. Cuvier, 1823).
Sphiggurus: F. Cuvier, 1825: 256 (misspelling of *Sphiggure* F. Cuvier, 1823; but see Remarks, below).
Coendu: Lesson, 1827: 290 (misspelling of *Coendou* Lacépède, 1799).
Synethere: Lesson, 1827: 291 (misspelling of *Sinethere* F. Cuvier, 1823).
Sinetheres: J. Fischer, 1829: 369 (misspelling of *Sinethere* F. Cuvier, 1823).
Cercolabes Brandt, 1835: 391; type species *Hystrix prehensilis* Linnaeus, 1758 (proposed as a replacement name for *Coendou* Lacépède, 1799).

Synoetheres: Lund, 1841: 99 (misspelling of *Sinethere* F. Cuvier, 1823).
Sphingurus: Tschudi, 1844: 185 (misspelling of *Sphiggure* F. Cuvier, 1823).
Echinoprocta Gray, 1865: 321; type species *Erethizon* (*Echinoprocta*) *rufescens* Gray, 1865, by monotypy.
Cryptosphingurus Miranda Ribeiro, 1936: 971; type species *C. villosus* (F. Cuvier, 1823, by original designation).

CONTENTS: Thirteen valid species as listed below.

REMARKS: The technical history of erethizontid generic nomenclature has been reviewed elsewhere (Tate, 1935; Alberico et al., 1999) and need not be repeated here. Although some recent authors (notably Woods and Kilpatrick, 2005) persist in recognizing *Coendou, Echinoprocta,* and *Sphiggurus* as valid genera, there is no compelling evidence that these are reciprocally monophyletic taxa. Bonvicino et al. (2002) suggested that available karyotypic data support the recognition of *Coendou* and *Sphiggurus* as distinct genera, but the chromosomal traits discussed by those authors—diploid numbers and fundamental numbers (table 2)—are phylogenetically uninterpretable in the absence of chromosome arm homologies. Molecular analyses that seem to recover *Coendou* and *Sphiggurus* as distinct clades (also in Bonvicino et al., 2002) do not, in fact, support this interpretation because the analyzed data include cytochrome-*b* sequences from misidentified specimens (see the account for *C. bicolor,* below). The phenotypic evidence for recognizing *Sphiggurus* as distinct from *Coendou* is inconclusive because no erethizontid morphological dataset has been analyzed phylogenetically, nor does any morphological character appear to diagnose either taxon (table 3). In effect, there seems to be no basis for meaningful generic distinctions among the species here referred to *Coendou.*

The generic name that Cuvier (1823) originally spelled *Sphiggure* has usually been spelled *Sphiggurus* following Cuvier (1825). Palmer (1904) claimed that *Sphiggure* was only used as a vernacular name, but Cuvier (1823) repeatedly employed this spelling in the same technical context (both alone and in binomial combination) and set in the same special typeface that he used for *Erethizon,* another genus named as new in the same work and universally accepted by authors as available from 1823. Although *Sphiggurus* is an incorrect subsequent spelling in the technical sense of the International Code of Zoological Nomenclature, it is the spelling in prevailing usage today and is therefore to be maintained (ICZN, 1999: Article 33.3.1).

Coendou bicolor (Tschudi, 1844)

Sphingurus bicolor Tschudi, 1844: 186; type locality "in den Urwäldern zwischen den Flüssen Tullumayo und Chanchamayo," Junín, Peru.
Coendou simonsi Thomas, 1902a: 141; type locality "Charuplaya, 1400 m," Cochabamba, Bolivia.
Coendou (*Coendou*) *bicolor*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *simonsi*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *bicolor bicolor*: Ellerman, 1940: 187 (name combination).
Coendou (*Coendou*) *bicolor simonsi*: Ellerman, 1940: 187 (name combination).

DISTRIBUTION: Based on specimens examined, *Coendou bicolor* occurs along the eastern Andean foothills and in adjacent Amazonian lowland forest from the Peruvian department of

TABLE 2. Karyotypic Variation among Erethizontids[a]

	$2n$[b]	FN[c]	Reference
Chaetomys subspinosus	52	76	Vilela et al. (2009)
Erethizon dorsatum	42	74	Benirschke (1968)
Coendou prehensilis	74	82	Lima (1994)
Coendou rothschildi	74	82	George & Weir (1974)
"*Sphiggurus*" *insidiosus*	62	76	Lima (1994)
"*Sphiggurus*" *melanurus*	72	76	Bonvicino et al. (2002)
"*Sphiggurus*" *pruinosus*	42	76	Concepción & Molinari (1991)
"*Sphiggurus*" *villosus*	42	75, 76	Bonvicino et al. (2000)

[a] Taxonomy follows Bonvicino et al. (2000).
[b] Diploid number.
[c] Fundamental number.

San Martín southward to northeastern Bolivia (Beni); an apparently isolated population occurs in relictual montane forest on the west side of the Andes in northern Peru (Cajamarca). The species is also credibly reported from northwestern Argentina (Jujuy; Lucero, 1987), but published reports of *C. bicolor* from the Peruvian department of Amazonas (Patton et al., 1982), Brazil (Lara et al., 1996), Ecuador (Tirira, 1999), Colombia (Alberico et al., 1999), and Venezuela (Linares, 1998) are based on misidentifications (see Remarks, below).

Remarks: I have not personally examined the holotype of *Coendou bicolor,* but several specimens from Chanchamayo (BMNH 5.11.2.20, 5.11.2.21; FMNH 65799, 65800) correspond closely to Tschudi's original description and can be considered topotypes. This material, together with other referred specimens from Peru and Bolivia, represents a large species (table 4) that lacks emergent fur and (with one known exception) has only bicolored quills. Additionally, the quills of the nape, shoulders, and upper back are much longer (80–90 mm) than those of the lower back and rump (≤ 50 mm). On museum skins, the overlapping blackish parts of the long anterior quills conceal the yellowish quill bases over the nape, shoulders and most of the dorsal surface, forming a visually conspicuous blackish mantle that contrasts in color with a yellowish rump. Lowland specimens (e.g., AMNH 214610–214612) have relatively longer tails, larger hind feet, and wider nasal apertures than specimens collected in montane habitats, a common ecophenotypic trend in other species of Neotropical porcupines. Most adult skulls of *C. bicolor* have inflated frontal sinuses, but some subadults (e.g., AMNH 262271) and young adults (FMNH 65799) do not. In all the specimens I examined, the dorsal roof of the external auditory meatus is smooth.

By comparison, most specimens of *Coendou prehensilis* (the only other large porcupine in eastern Peru and Bolivia) have long tricolored (white-tipped) quills over the entire dorsal surface, and there is no distinct mantle of longer quills over the nape, shoulders, and upper back. Additionally, *C. prehensilis* tends to have much more inflated frontal sinuses than *C. bicolor* (the swelling often extending into the nasals and parietals), and the mesopterygoid fossa does not penetrate as deeply between the tooth rows in most specimens of *C. prehensilis* as it does in most specimens of *C. bicolor* (table 5).

TABLE 3. Selected Morphological Traits of 13 Species of *Coendou*[a]

	Long fur	Quills	Bristle-quills[b]	LT/HBL[c]	Frontal sinuses[d]	EAM roof[e]	MTR (mm)[f]
bicolor	absent	bicolored	absent	ca. 90–105%	inflated	smooth	20.1 (19.4–21.3) 9
*ichillus**	absent	bicolored	tricolored	ca. 85%	not inflated	smooth	14.4 (14.0–15.2) 3
*insidiosus**	present	bicolored	absent	ca. 65%	not inflated	smooth	14.0 (13.6–14.3) 4
*melanurus**	present	bicolored	absent	ca. 95%	not inflated	strongly keeled	17.6 (15.7–19.4) 7
*mexicanus**	present	bicolored	absent	ca. 65–80%	inflated[g]	strongly keeled	19.6 (18.2–21.8) 26
nycthemera	absent	bi- & tricolored	absent	ca. 90%	not inflated	smooth	15.3 (14.1–16.3) 25
prehensilis	absent	bi- & tricolored	absent	ca. 100%	strongly inflated	weakly keeled	20.1 (18.6–22.2) 26
*pruinosus**	present	bicolored	tricolored	ca. 50–70%	not inflated	weakly keeled	15.1 (14.3–15.8) 12
quichua	absent	bi- & tricolored	absent	ca. 55–90%	not inflated	strongly keeled	17.8 (16.8–18.6) 29
*roosmalenorum**	present	bicolored	tricolored	ca. 85%	not inflated	weakly keeled	13.0 (12.6–13.4) 2
rufescens	absent	bi- & tricolored	absent	ca. 40%	not inflated	smooth	17.5 (16.7–19.2) 13
*spinosus**	present	bi- & tricolored	absent	ca. 75%	not inflated	smooth	15.9 (15.1–17.0) 23
vestitus	present	bicolored	bicolored	ca. 50%	not inflated	weakly keeled	15.5 (14.7–16.4) 7

[a] Tabulated traits are modal conditions (the phenotype observed in most examined specimens); rare exceptions are noted in species accounts or in cited references. Species marked with an asterisk (*) were referred to the genus *Sphiggurus* by Woods and Kilpatrick (2005), who also referred *rufescens* to the genus *Echinoprocta*.

[b] Nondefensive quills with long wirelike tips (Voss and da Silva, 2001: fig. 1).

[c] Table entries are mean values for length of tail divided by length of head and body × 100, rounded to the nearest 5%. Apparently erroneous collector's measurements were omitted from the data used to calculate these values. Data are from Voss and Angermann (1997), Voss and da Silva (2001), Voss et al. (2001), and this report. Ranges are provided for species with noteworthy geographic variation (see text).

[d] Subject to individual variation in several species.

[e] Roof of the external auditory meatus. Contrasting character states are illustrated in Voss et al. (2001: fig. 70).

[f] Adult maxillary toothrow length (a proxy for size). Tabulated sample statistics include the mean, the observed range (in parentheses) and the sample size.

[g] In Mexican specimens; see text for remarks on geographic variation.

TABLE 4. Measurements (mm) of Adult Specimens of *Coendou bicolor*

		Bolivia			
	Peru[a]	AMNH 214610♀	AMNH 214611♀	AMNH 214612♀	BMNH 2.1.1.103♀[b]
HBL	457 (405–500) 5	493	473	475	425
LT	422 (345–480) 5	540	500	490	335
HF	84 (76–95) 5	94	96	95	80
CIL	89.5 (85.3–94.1) 5	87.1	94.0	89.7	85.2
LD	24.4 (22.0–27.7) 5	23.7	26.7	26.5	23.7
MTR	20.5 (19.7–21.3) 5	19.5	19.9	19.4	20.1
LM	14.9 (14.4–15.2) 5	14.2	14.5	13.8	14.5
BP4	5.8 (5.6–6.0) 5	6.0	6.0	5.4	5.9
BM1	5.3 (4.9–5.7) 5	5.2	5.4	5.2	5.2
APB	6.1 (5.5–6.6) 5	5.7	6.4	6.0	7.4
PPB	8.8 (8.0–9.8) 5	—	8.1	9.0	10.9
PZB	51.2 (49.8–53.7) 4	51.9	53.0	52.2	51.0
HIF	14.0 (12.6–16.1) 5	14.9	15.2	14.5	13.9
ZL	33.3 (31.6–34.4) 4	35.0	35.8	34.8	32.9
LN	28.7 (27.6–29.7) 5	30.9	27.7	29.3	28.2
BNA	18.6 (18.1–19.1) 4	20.2	20.8	18.8	17.0
BB	39.7 (38.3–40.8) 5	39.7	39.6	38.8	37.6
DI	4.1 (3.8–4.5) 5	4.2	4.1	3.9	3.8
BIT	6.2 (6.0–6.4) 5	5.9	5.4	5.4	5.5

[a] The sample mean, the observed range (in parentheses) and the sample size are provided for each measurement of the following series: AMNH 147500; BMNH 97.10.3.13, 5.11.2.21; FMNH 65799, 65800 (4 males, 1 female).
[b] Type of *simonsi*.

Cabrera (1961) treated several nominal taxa as subspecies of *Coendou bicolor,* including *quichua* (a valid species), *richardsoni* (a synonym of *quichua*), *sanctaemartae* (a synonym of *prehensilis*), and *simonsi.* Although I also treat *simonsi* as a synonym of *C. bicolor,* the type (BMNH 2.1.1.103) differs from all other specimens referred to this species by having tricolored (orange-tipped) quills over its head, nape, shoulders, and lower flanks. Additional material from montane habitats in Cochabamba, where the holotype was collected at 1400 m (Thomas, 1902a), would help determine whether the tricolored quills of this specimen are an individual peculiarity or represent a distinct local phenotype.

The Peruvian material that Patton et al. (1982) reported as *Coendou bicolor* from Huampami in the department of Amazonas consists of four specimens (MVZ 153571, 153572, 155199, 155201) that exhibit the suite of traits I associate with *C. prehensilis,* as do both of the specimens (MNFS 439, 1016) that Lara et al. (1996) identified as *C. bicolor* from western Brazil (Acre and Amazonas).[2] A juvenile porcupine (LSU 16745) from Balta (in easternmost Uca-

[2] Cytochrome-*b* sequences obtained from Lara et al.'s (1996) misidentified material (with GenBank accession numbers U34851 and U34852) were subsequently analyzed as *C. bicolor* by Bonvicino et al. (2002), Vilela et al. (2009), and Leite et al. (2011). Results of those analyses that seem to support the reciprocal monophyly of *Coendou* (supposedly represented by *C. bicolor* and *C. prehensilis*) versus "*Sphiggurus*" merely support the monophyly of *C. prehensilis* as understood in this report.

yali department, Peru) that Voss and Emmons (1996: 105) reported as "*Coendou* cf. *bicolor*" is another misidentified example of *C. prehensilis.* The illustrations of *C. bicolor* in Emmons and Feer (1997: pl. 28) and Tirira (1999: pl. 20) likewise depict *C. prehensilis* as recognized herein.

TABLE 5. Comparison of Mesopterygoid Fossa Penetration between the Cheektooth Rows of Adult and Subadult Specimens of *Coendou bicolor* and *C. prehensilis*[a]

Mesopterygoid penetration	*bicolor*	*prehensilis*[a]
Between M2s	9	1
To M2/M3 commissure	0	3
Between M3s	3	15

[a] From Peru, Bolivia, and central Brazil.

Linares (1998) did not list the specimens that he identified as *Coendou bicolor* from the Maracaibo Basin of western Venezuela, but two from Las Mesas in Estado Táchira (USNM 443409, 443410) appear to represent the phenotype he described. These are large animals (TL = ca. 885 mm for USNM 443410) with bicolored quills that, lying flat on the stuffed skin, give the impression of a completely black porcupine. However, unlike *C. bicolor,* the quills of these specimens are not conspicuously longer on the shoulders and upper back than on the lower back and rump, and the dorsal cranial sinuses are highly inflated. Except in coloration, these specimens more closely resemble geographically adjacent populations of *Coendou prehensilis,* and I therefore follow Handley (1976) in referring them to that species.

I have not examined either of the two Colombian specimens that Alberico et al. (1999) implausibly identified as *Coendou bicolor.* One specimen was said to consist of a skin and skull from Provincia (7°25′N, 73°26′W) in the western foothills of the Cordillera Oriental, and the other of a skull only from Tolú (9°31′N, 75°35′W) on the eastern shore of the Golfo de Morrosquillo. It is possible that the former is a melanistic example of *C. prehensilis* (resembling the Venezuelan material discussed in the previous paragraph), and that the latter is an unusually large example of *C. quichua,* but these conjectures should be tested by reexamining his material.

I have not examined all the Bolivian specimens that Anderson (1997) identified as *Coendou bicolor,* but at least some of them belong to other species. The specimen from Incachaca (CM 5255), for example, is the first known Bolivian example of *C. rufescens* (see below). Therefore, the material he listed from the Colección Boliviana de Fauna (in La Paz) and the Estación Biológica Doñana (in Seville) should be checked for diagnostic traits of this species before the localities in question are used for geographic range mapping, niche modeling, or other ecogeographic analyses.

Specimens examined (N = 18): **Bolivia**—*Beni,* Puerto Caballo (AMNH 214615), Río Mamoré (AMNH 214610–214612), Yucumo (AMNH 262271); *Cochabamba,* Charuplaya (BMNH 2.1.1.103 [holotype of *simonsi*]). **Peru**—no other locality information (ANSP 121); *Cajamarca,* 2.5 km N Monte Seco (MUSM 9398); *Huánuco,* Hacienda San Juan de Cuchera (FMNH 41204), Tingo María (FMNH 91303); *Junín,* Chanchamayo (BMNH 5.11.2.20, 5.11.2.21; FMNH 65799, 65800), Vitoc (BMNH 97.10.3.13); *Madre de Dios,* Reserva Cuzco Amazónico (KU 144560); *San Martín,* Área de Conservación Municipal Mishquiyacu-Rumiyacu y Almendra (FMNH 203679); *Ucayali,* Río Alto Ucayali (AMNH 147500).

Coendou ichillus Voss and da Silva, 2001

Coendou ichillus Voss and da Silva, 2001: 17; type locality Río Pastaza, Provincia Pastaza, Ecuador.
Sphiggurus ichillus: Woods and Kilpatrick, 2005: 1548 (name combination).

DISTRIBUTION: All known specimens and reliable sight records of *Coendou ichillus* are from the rainforested lowlands of eastern Ecuador and northeastern Peru (Voss and da Silva, 2001), but it would be reasonable to expect this species to occur throughout most of northwestern Amazonia (north of the Amazon and west of the Rio Negro).

REMARKS: This species may be closely related to *Coendou pruinosus, C. roosmalenorum,* and *C. vestitus,* all of which also have bristle-quills in addition to ordinary defensive quills and soft fur in their dorsal pelage. A detailed morphological description of *C. ichillus* and relevant comparisons with congeneric taxa were provided by Voss and da Silva (2001). A recently published photograph of the skin of an Ecuadorean porcupine in the Gothenburg Museum of Natural History (Johansson and Högström, 2008) is captioned as "*Sphiggurus ichillus,*" but the specimen in question is unambiguously identifiable by its very short tail and reddish quills as *Coendou rufescens* (see below).

SPECIMENS EXAMINED: In addition to the material listed by Voss and da Silva (2001), I subsequently examined an uncataloged specimen of *Coendou ichillus* from Iquitos, Peru (with field number CLH 4709) in the Museum of Texas Tech University (Lubbock, TX).

Coendou insidiosus (Olfers, 1818)

H[*ystrix*]. *insidiosa* Olfers, 1818: 211; type locality "Brazil," most probably Salvador in northeastern Bahia (Voss and Angermann, 1997).
Cercolabes pallidus Waterhouse, 1848: 434; type locality unknown (originally said to be from the "West Indies," but presumably from southeastern Brazil; Voss and Angermann, 1997).
Synetheres (*Sphiggurus*) *pallidus*: Trouessart, 1881: 184 (name combination).
Coendu pallidus: Trouessart, 1897: 622 (name combination).
Coendu insidiosus: Trouessart, 1897: 623 (name combination).
Coendou (*Sphiggurus*) *insidiosus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *pallidus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *pallidum*: Ellerman, 1940: 187 (misspelling of *pallidus* Waterhouse, 1848).
Coendou (*Sphiggurus*) *insidiosus insidiosus*: Cabrera, 1961: 600 (name combination).
Sphiggurus insidiosus: Husson, 1978: 484 (part, not including referred Surinamese specimens; name combination).
Sphiggurus pallidus: Woods, 1993: 776 (name combination).

DISTRIBUTION: I have only examined specimens from the Brazilian state of Bahia, but the species is said to occur in moist forests from southern Sergipe to northern Rio de Janeiro (roughly between 11° and 22° S latitude), including easternmost Minas Gerais (Santos et al., 1987; Oliver and Santos, 1991).

REMARKS: The synonymy provided above does not include name combinations that represent erroneous applications of the epithet *insidiosus* to other *Coendou* species (e.g., *C.*

melanurus, C. spinosus). The original authorship of this species has often been misattributed; see Voss and Angermann (1997) for an explanation of its tediously complex nomenclatural history, for diagnostic comparisons with *C. spinosus,* and for a detailed description of Olfers' (1818) original material. Diagnostic comparisons of *C. insidiosus* with *C. melanurus* were illustrated by Voss et al. (2001). Photographs of live individuals of *Coendou insidiosus* are in Oliver and Santos (1991).

SPECIMENS EXAMINED: See Voss and Angermann (1997).

Coendou melanurus (Wagner, 1842)

Cercolabes melanurus Wagner, 1842: 360; type locality "Rio Negro [Barra]" (= Manaus), Amazonas, Brazil.
Sphiggurus melanurus Gray, 1842: 262; type locality "Brazil."
Synetheres (*Sphiggurus*) *melanurus*: Trouessart, 1881: 184 (name combination).
Coendu melanurus: Trouessart, 1897: 622 (name combination).
Coendou (*Sphiggurus*) *melanurus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *insidiosus melanurus*: Cabrera, 1961: 601 (name combination).
Sphiggurus melanura: Bonvicino et al., 2002 (epithet spelled with incorrect gender).

DISTRIBUTION: Apparently throughout the northeastern Amazonian lowlands (north of the Amazon and east of the Orinoco-Cassiquiare–Rio Negro), including eastern Venezuela, Guyana, Surinam, French Guiana, and northern Brazil (Voss et al., 2001: fig. 66).

REMARKS: This species was misidentified as or treated as a synonym or subspecies of *Coendou insidiosus* by Cabanis (1848), Cabrera (1961), Husson (1978), and Woods (1993), among others. Voss et al. (2001) provided a detailed description of *C. melanurus* and illustrated diagnostic comparisons with *C. insidiosus.* Reports of *C. melanurus* from Ecuador and Colombia (Emmons and Feer, 1997; Alberico et al., 1999; Tirira, 1999) were based on misidentified material of *C. ichillus* and *C. pruinosus,* respectively (Voss and da Silva, 2001).

SPECIMENS EXAMINED: See Voss et al. (2001: 136).

Coendou mexicanus (Kerr, 1792)

Hystrix mexicana Kerr, 1792: 214; type locality "the mountains of Mexico."
Cercolabes liebmani Reinhardt, 1844: 241; type locality in the Mexican state of Veracruz (see Remarks, below).
Synetheres mexicanus: Alston, 1880: 170 (name combination).
Coendou mexicanum: Miller and Rehn, 1901: 173 (name combination with misspelled epithet).
Coendou mexicanus yucataniae Thomas, 1902b: 249; type locality "Yucatan (probably near Izamal)."
Coendou laenatus Thomas, 1903a: 381; type locality "Boquete, 5000 feet" in Chiriquí province, Panama.
Coendou (*Sphiggurus*) *laenatus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *mexicanus mexicanus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *mexicanus yucataniae*: Tate, 1935: 307 (name combination).

TABLE 6. Measurements (mm) of Adult Specimens of *Coendou mexicanus* from Mexico and Panama[a]

	Mexico (Oaxaca)[b]	Panama (Chiriqui)[c]
HBL	412 ± 24 (375–460) 17	418 (390–452) 6
LT	360 ± 39 (290–440) 17	263 (220–319) 6
HF	82 ± 5 (73–95) 17	69 (67–71) 5
CIL	85.4 ± 4.8 (76.6–95.6) 17	79.5 (75.8–85.7) 8
LD	24.4 ± 2.0 (21.0–27.7) 18	22.6 (19.3–25.4) 8
MTR	19.8 ± 0.9 (18.2–21.8) 18	19.0 (18.2–19.8) 8
LM	14.3 ± 0.7 (12.9–15.8) 18	14.0 (13.5–14.5) 8
BP4	6.0 ± 0.4 (5.0–6.5) 18	5.5 (5.1–6.1) 8
BM1	5.4 ± 0.3 (4.8–5.9) 18	5.1 (4.8–5.5) 8
APB	5.4 ± 1.1 (3.6–7.4) 18	5.9 (4.6–7.1) 8
PPB	7.1 ± 1.0 (5.6–8.8) 15	7.9 (7.1–8.6) 8
PZB	48.6 ± 1.6 (45.7–50.9) 16	47.9 (45.7–50.0) 7
HIF	13.0 ± 0.7 (11.3–14.1) 18	12.5 (11.3–14.1) 8
ZL	33.3 ± 1.6 (30.6–36.8) 18	31.8 (29.9–33.4) 8
LN	31.8 ± 3.5 (27.5–38.7) 11	25.9 (24.7–27.4) 4
BNA	17.1 ± 1.2 (14.4–19.1) 18	14.9 (14.2–15.5) 7
BB	35.6 ± 1.3 (33.9–39.0) 17	33.7 (31.4–34.8) 8
DI	4.3 ± 0.2 (4.0–4.8) 17	3.9 (3.7–4.1) 8
BIT	5.8 ± 0.3 (5.1–6.1) 15	5.5 (5.2–5.9) 6

[a] Tabulated statistics include the sample mean plus or minus one standard deviation (for $N \geq 10$), the observed range (in parentheses), and the sample size.

[b] AMNH 72450, 72452, 72454, 72455, 74677, 76196, 76197, 143969, 145983, 190417, 190419, 190421–190427 (9 males, 9 females).

[c] BMNH 3.3.3.94 (holotype of *laenatus*), 4.7.6.6; USNM 324113–324115, 396587, 520770, 539938 (1 male, 4 females, 3 sex unknown).

Coendou mexicanum laenatum: Goldman, 1920: 133 (name combination and misspelled epithets).
Sphiggurus mexicanus: Woods, 1993: 776 (name combination).

DISTRIBUTION: From San Luis Potosí in eastern Mexico (Dalquest, 1950) and Michoacán in western Mexico (Monterrubio-Rico et al., 2010) southward throughout most of Central America to western Panama (Bocas del Toro and Chiriquí; Handley, 1966). According to Monterrubio-Rico et al. (2010), *Coendou mexicanus* occurs from sea level to at least 2350 m.

REMARKS: The best available descriptions of this species are in Waterhouse (1848), Goodwin (1946), and Emmons and Feer (1997); cranial photographs are in Goodwin (1969); and measurement data are provided in table 6. This is the only species of *Coendou* with dorsal pelage composed of long, uniformly soft, black fur; short (< 50 mm) bicolored quills; and (usually) a well-developed bony ridge on the roof of the external auditory meatus. By comparison, the black fur of *Coendou melanurus*—another species with short bicolored quills—is abundantly streaked with yellowish or whitish guard hairs (Voss et al., 2001: fig. 67), and the blackish fur of *C. vestitus* is not uniformly soft because it is intermingled with the wiry tips of long bristle-quills (Voss and da Silva, 2001: fig. 1). Some populations of *C. spinosus* have predominantly blackish fur, but the pelage of that species is frosted with yellow or orange because the individual hairs have pale tips; *C. spinosus* also differs from *C. mexicanus* by having tricolored quills

(with yellow or orange tips) over its head and forequarters, and it has a smooth-roofed external auditory meatus. *Coendou quichua* (including *rothschildi*; see below), the only other species of porcupine that occurs in Central America, differs from *C. mexicanus* by lacking emergent fur (appearing completely spiny) and by having tricolored quills (usually white-tipped in Panamanian specimens) scattered throughout its dorsal pelage. The contrasting external features of *C. mexicanus* and *C. quichua* are clearly illustrated in Reid (1997: pl. 32).

Coendou mexicanus is geographically variable. Throughout its range, highland specimens usually have longer and denser fur than lowland specimens, and some populations differ in size and qualitative cranial traits. Panamanian specimens (including the holotype of *laenatus*), for example, have less inflated frontal sinuses than Mexican specimens, and also have much shorter tails, smaller hind feet, and narrower nasal apertures (table 6). A careful study of geographic variation in these characters would be welcome, as would complementary phylogeographic analyses of mtDNA sequence variation within this widespread species.

According to Hall (1981: 854), the type locality of *Cercolabes liebmani* is "Mexico," but both of Reinhardt's syntypes were collected in the state of Veracruz: one from Mirador (19°13′N, 96°51′W) and the other from the nearby town of "St. Francisco Tenampa" (= Tenampa; 19°15′N, 96°53′W). Both specimens are still preserved in the Zoological Museum of the University of Copenhagen (M. Andersen, personal commun.). At the moment, there seems to be no reason to designate a lectotype for this nominal taxon, nor to designate a neotype for *Hystrix mexicana*. In addition to the junior synonyms listed above, the unavailable epithet "*novae-hispaniae*" was used for this species by Waterhouse (1848) and other 19th-century authors (Tate, 1935).

Specimens examined ($N = 76$): **Belize**, *Cayo District,* 2 miles from Georgeville (BMNH 1965.3903). **Costa Rica**—*Cartago,* Irazú (FMNH 34993, 34994), Paso Ancho (AMNH 139253); *Limón,* "Río Teribe" (= Río Terebé; USNM 539937); *Puntarenas,* Barranca (AMNH 135976); *San José,* Cerro de la Muerte (UMMZ 115461), Escazu (AMNH 131727, 137991, 137992). **El Salvador**—*San Miguel,* Lake Olomega (UMMZ 110952). **Guatemala**—no other locality data (USNM 61243). **Honduras**—*Atlántida,* Tela (MCZ 26086); *Francisco Morazán,* Tegucigalpa (AMNH 123274, 123275, 127572). **Mexico**—*Oaxaca,* Concepción (AMNH 145983), Llano Grande (USNM 72450–72455, 74677), Mogone (AMNH 143969), 16 mi N Matías Romero (AMNH 186427), 20 mi NW La Ventosa (AMNH 190417–190427), Santa Efigenia (USNM 76196, 76197); *Veracruz,* Catemaco (USNM 65963), Minatitlán (USNM 79659), Orizaba (MCZ 6421), 24 mi S Veracruz (AMNH 204281, 204283), Tenochtitlán (UMMZ 116343, 116344); *Yucatán,* probably near Izamal (BMNH 91.3.24.1 [holotype of *yucataniae*], Tekom (BMNH 52.378–52.380). **Nicaragua**—*Granada,* La Calera (USNM 339965, 339966); *Managua,* 12–17 km S Managua (USNM 332446, 332447, 334642, 334645, 334646, 334648); *Matagalpa,* Matagalpa (AMNH 28334), Uluce (AMNH 29821); *Nueva Segovia,* Ocotal (AMNH 28484, 28485); *Rivas,* Hacienda Amaya (USNM 337900). **Panama**—*Chiriquí,* Boquete (BMNH 3.3.3.94 [holotype of *laenatus*], 4.7.6.6; MCZ 11038), Cerro Punta (USNM 324111–324115, 519702), El Volcán (ANSP 18847; USNM 396587, 520770), Río Candela (USNM 539938, 539939).

Coendou nycthemera (Olfers, 1818)

H[*ystrix*]. *nycthemera* Olfers, 1818: 211; type locality "Brazil," probably somewhere on the south (right) bank of the Amazon below Óbidos (Voss and Angermann, 1997).
Cercolabes nycthemera: Waterhouse, 1848: 417 (name combination).
Synetheres (*Synetheres*) *nycthemera*: Trouessart, 1881: 183 (name combination).
Coendu nycthemera: Trouessart, 1897: 622 (name combination).
Coendou (*Sphiggurus*) *nycthemera*: Tate, 1935: 307 (name combination).
Coendou (*Coendou*) *nycthemera*: Ellerman, 1940: 187 (name combination).
Coendou koopmani Handley and Pine, 1992: 238; type locality Belém, Pará, Brazil.
Coendou nycthemerae: Eisenberg and Redford, 1999: 450 (misspelling).

DISTRIBUTION: Specimens of *Coendou nycthemera* have been collected from the Rio Madeira eastward along the right (south) bank of the Amazon to Marajó Island in the Brazilian states of Amazonas and Pará (Handley and Pine, 1992). Interviews with indigenous hunters suggest that the range of this species also extends into the adjacent Atlantic coastal watershed of Maranhão (Oliveira et al., 2007).

REMARKS: The authorship of this species has often been misattributed; see Voss and Angermann (1997) for nomenclatural details. Olfers' (1818) original Latin description of *Coendou nycthemera* is virtually useless, but detailed morphological descriptions were provided by Handley and Pine (1992), Emmons and Feer (1997), and Voss and Angermann (1997). This species has historically been confused with *C. bicolor,* a substantially larger western Amazonian species.

SPECIMENS EXAMINED: See Voss and Angermann (1997).

Coendou prehensilis (Linnaeus, 1758)

Hystrix prehensilis Linnaeus, 1758: 57; type locality "Mata Xanguá, Usina Trapiche, municipality of Sirihaém, state of Pernambuco, Brazil, 8°38′50″S, 35°10′15″W, elevation 100 m" (fixed by neotype selection; Leite et al., 2011).
Coendou prehensilis: Lacépède, 1799: 11 (name combination).
Coendou longicaudatus Daudin, 1802: 172; type locality Cayenne, French Guiana (based on the "Coendou à longue queue" of Buffon).
Hystrix cuandu Desmarest, 1822: 346; type locality "Le Brésil, la Guyane, l'île de la Trinité."
S[*inethere*]. *prehensilis*: F. Cuvier, 1823: 433 (name combination).
Cercolabes (*Synetheres*) *prehensilis*: Brandt, 1835: 396 (name combination).
Cercolabes (*Synetheres*) *platycentrotus* Brandt, 1835: 399; type locality "America australis?" (see Remarks, below).
Cercolabes prehensilis: Wagner, 1844: 29 (name combination).
Cercolabes boliviensis Gray, 1850: 380; type locality "Bolivia," apparently near Santa Cruz de la Sierra (see Remarks, below).
Cercolabes tricolor Gray, 1850: 381; type locality unknown (see Remarks, below).
Hystrix brandtii Jentink, 1879: 96; type locality "Surinam" (fixed by lectotype selection; Husson, 1978).

Synetheres (*Synetheres*) *boliviensis*: Trouessart, 1881: 183 (name combination).
Synetheres (*Synetheres*) *brandtii*: Trouessart, 1881: 183 (name combination).
Synetheres (*Synetheres*) *prehensilis*: Trouessart, 1881: 183 (name combination).
Coendu brandtii: Trouessart, 1897: 621 (name combination).
Coendu tricolor: Trouessart, 1897: 622 (name combination).
Coendu boliviensis: Trouessart, 1897: 622 (name combination).
Coendou centralis Thomas, 1904: 240; type locality "Chapada" (= Chapada dos Guimarães), Mato Grosso, Brazil.
Coendou sanctaemartae J.A. Allen, 1904: 411; type locality "Bonda, Santa Marta district, Colombia."
Coendou (*Coendou*) *prehensilis*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *boliviensis*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *brandtii*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *sanctaemartae*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *tricolor*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *centralis*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *platycentrotus*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *prehensilis prehensilis*: Ellerman, 1940: 187 (name combination).
Coendou (*Coendou*) *prehensilis boliviensis*: Ellerman, 1940: 187 (name combination).
Coendou prehensilis platycentrotus: Miranda Ribeiro, 1936: 971 (name combination).

DISTRIBUTION: *Coendou prehensilis* occurs from northern Colombia (Magdalena, Cesar, Bolívar) eastward across northern South America (including Venezuela and the Guianas; Handley, 1976; Husson, 1978) and southward throughout most of the forested cis-Andean lowlands of Ecuador, Peru, and Brazil to eastern Bolivia (Beni, Cochabamba, La Paz, Santa Cruz; Anderson, 1997), northwestern Argentina (Salta; Olrog, 1976), and eastern Paraguay (Concepción, Paraguarí; Yahnke et al., 1998). It seems probable that *C. prehensilis* also occurs in western Paraguay, but no specimens or sightings have apparently been reported from the region.

REMARKS: Because it was originally based on vernacular descriptions of several different species, Linnaeus's (1758) concept of *Hystrix prehensilis* was composite. Nineteenth-century usage followed Kerr (1792), who restricted the application of this name to the eastern Brazilian porcupine described by Marcgraf (1648). Thomas (1911) recommended that the type locality should be construed as Pernambuco, where Marcgraf (or Markgraf; see Whitehead, 1979) principally resided while he was in Brazil. Because Thomas's recommendation was not nomenclaturally binding, however, and because the porcupines currently referred to *Coendou prehensilis* may comprise more than one valid taxon, Leite et al. (2011) appropriately designated a neotype.[3]

The best descriptions of this species are in Husson (1978) and Leite et al. (2011), both of whom illustrate its distinctive external and craniodental morphology. This is a large, long-tailed porcupine, adult specimens of which appear to be completely spiny because they lack emergent fur; the longest dorsal quills (60–110 mm) of most specimens are tricolored (white-tipped), even over the rump; the frontal sinuses of adults and subadults are always inflated; the nasal

[3] Husson (1978: 483) had previously designated the animal illustrated by Marcgraf as the lectotype, but the specimen itself is not known to exist.

TABLE 7. Measurements (mm) of Adult Specimens of *Coendou prehensilis* from Northern Colombia and Central Brazil[a]

	Northern Colombia[b]	Central Brazil[c]
HBL	451 ± 25 (403–508) 15	504 (480–530) 7
LT	453 ± 31 (365–487) 15	514 (480–550) 7
HF	90 ± 4 (82–97) 15	97 (88–105) 6
CIL	84.5 ± 3.7 (77.8–91.8) 16	93.1 ± 2.3 (89.5–96.6) 10
LD	22.0 ± 1.3 (20.0–24.6) 16	25.8 ± 1.8 (23.0–28.4) 11
MTR	19.4 ± 0.5 (18.6–20.4) 15	21.1 ± 0.9 (19.3–22.2) 11
LM	14.3 ± 0.4 (13.3–14.8) 15	15.6 ± 0.7 (14.3–16.6) 11
BP4	5.7 ± 0.2 (5.3–6.1) 16	6.0 ± 0.3 (5.3–6.4) 11
BM1	5.4 ± 0.2 (5.1–5.7) 15	5.9 ± 0.3 (5.4–6.3) 11
APB	6.5 ± 0.6 (5.2–7.5) 16	7.3 ± 0.9 (5.8–8.7) 11
PPB	8.7 ± 0.7 (7.7–10.0) 14	10.3 ± 1.0 (8.9–12.1) 11
PZB	50.1 ± 2.0 (46.8–53.3) 14	55.7 ± 2.1 (51.5–58.2) 10
HIF	12.2 ± 0.8 (10.2–13.5) 16	14.8 ± 1.1 (13.4–15.8) 11
ZL	32.9 ± 1.5 (30.7–35.8) 16	36.8 ± 1.4 (34.5–39.3) 10
LN	30.0 ± 1.4 (27.5–32.0) 11	33.1 ± 2.0 (31.0–36.5) 6
BNA	19.0 ± 0.9 (17.3–20.3) 13	23.6 ± 0.9 (22.0–25.2) 9
BB	37.0 ± 0.9 (35.2–39.2) 16	39.1 ± 1.9 (35.9–41.9) 10
DI	4.2 ± 0.2 (3.8–4.5) 16	4.5 ± 0.2 (4.1–4.8) 11
BIT	6.1 ± 0.5 (5.6–7.4) 15	6.2 ± 0.5 (5.4–6.9) 9

[a] Tabulated statistics include the sample mean plus or minus one standard deviation (for $N \geq 10$), the observed range (in parentheses), and the sample size.

[b] From Cesar and Magdalena: AMNH 15459, 15460, 23471; USNM 281897, 281898, 281901–281906, 281908, 281909, 281912, 281914, 281916 (6 males, 10 females).

[c] From Minas Gerais, Goiás, and Mato Grosso: AMNH 1256/356, 134062, 134064, 134067, 134069, 134070; ANSP 4802; BMNH 1.11.3.70, 3.7.7.101, 3.7.7.102; ZMUC 521 (5 males, 3 females, 3 sex unknown).

aperture is very wide; and the upper incisors are distinctly procumbent. As remarked by Leite et al. (2011), *Coendou prehensilis* may be a complex of closely related forms, but I have not discovered any morphological character by which different nominal taxa herein treated as subjective junior synonyms can be unambiguously diagnosed. The following remarks summarize known patterns of geographic variation in phenotypic traits and discuss the application of available names should any taxa merit formal recognition in future revisionary studies.

The largest specimens I have measured are from central Brazil and eastern Bolivia (where local populations have been variously identified by authors as *platycentrotus, boliviensis, brandtii,* or *centralis*) and the smallest are from northern Colombia (table 7). The latter were described as a distinct species (*sanctaemartae*) by Allen (1904), who claimed that they were about one-third smaller than Brazilian specimens, but Allen underestimated the mature size of this nominal taxon by failing to take ontogenetic variation into account (two of his paratypes [AMNH 24372, 24373] are subadults). In fact, measurements of adult specimens from northern Colombia overlap with those of central Brazilian specimens in most dimensions (BNA is the sole exception), and these samples do not appear to differ in other external or craniodental features.

The epithet *sanctaemartae* is available should populations of *Coendou prehensilis* in northern South America merit subspecific recognition, but *longicaudatus* (from French Guiana) is an older name. Although I have not measured French Guianan material nor directly compared any specimens from the Guianas with northern Colombian material, measurements of Surinamese specimens (in Husson, 1978) suggest that Guianan populations are closer in size to central Brazilian than to northern Colombian animals. A third northern South American name, *brandtii,* is a junior synonym of *longicaudatus* (see Husson, 1978).[4] In the event that any *prehensilis*-like northern South American porcupine merits recognition as a distinct taxon, a French Guianan neotype should be designated to fix the application of *longicaudatus.*

The name *platycentrotus* is based on a mummified specimen (formerly preserved in fluid) of unknown geographic origin. Its quills are longitudinally grooved (Brandt, 1835: pl. II), possibly a developmental pathology or an artifact of having once been fluid filled and subsequently dessicated. In either case, they are surely not taxonomically diagnostic, and the specimen otherwise resembles ordinary material of *Coendou prehensilis.* Although the name has been applied to central Brazilian populations based on conjectures about where the type might have been collected (Cabrera, 1961), it seems best regarded as a nomen dubium.

Gray (1850) named *boliviensis* based on a specimen obtained by one Mr. Bridges, who is said to have collected it in the vicinity of Santa Cruz de la Sierra in eastern Bolivia (Waterhouse, 1848: 411). The holotype consists of the skin and skull of a very old animal, which plausibly accounts for its unusually large skull (CIL = 105 mm) and proportionately small cheek teeth (worn down below the widest parts of their crowns). Another distinctive trait of this specimen, its grooved upper incisors, appears to be an individual peculiarity. In all other respects, Mr. Bridge's porcupine closely resembles others collected in eastern Bolivia, as well as those from the contiguous dry forests of central Brazil.

Gray (1850) also proposed the name *tricolor* for a specimen of unknown origin that was said to be darker than other *prehensilis*-like specimens then preserved at the British Museum. Although the type of *tricolor* is, in fact, darker than other mid 19th-century BMNH specimens, it is not sufficiently distinctive to justify the use of this name for any known geographic form of *Coendou prehensilis* in the absence of definite information about where it was collected. According to Moojen (1952: 104), the type locality of *tricolor* is Igarapé-açu (near Belém in the Brazilian state of Pará), but I am not aware of any documentary evidence that the type was actually collected there.

Thomas (1904) named *centralis* based on a specimen with less swollen frontal sinuses than other sympatrically collected specimens that he referred to *brandtii.* Although Thomas believed the observed disparity in sinus inflation "too great to be due to individual variation" (op. cit.: 241), cranial differences between BMNH 3.7.7.102 and other porcupines from Chapada dos Guimarães do not exceed those that can be found within several series of *Coendou prehensilis*

[4] Jentink's (1879) description of *brandtii* was based on three specimens: one collected in Brazil by Georg Heinrich von Langsdorff (Barman, 1971), another obtained from the Rotterdam zoo, and a third collected in Surinam. Abramov and Baranova (2008) assumed that Langsdorff's Brazilian specimen (ZINRAS O.6593) was the holotype, but Husson (1978: 484) had earlier designated the Surinamese specimen as lectotype.

from other localities, such as the AMNH material from Anápolis or the USNM material from Valledupar. To be fair, such large series were unavailable in Thomas's day, so the individual variability of the species could not have been accurately assessed at the time. In effect, *centralis* (the only name definitely based on a central Brazilian specimen) is taxonomically indistinguishable from the eastern Bolivian phenotype to which the older name *boliviensis* unambiguously applies (see above). Collectively, this material (from eastern Bolivia and central Brazil) is conspicuously paler than the Pernambuco neotype of *prehensilis* (illustrated by Leite et al., 2011: figs. 2, 3), and side-by-side comparisons might reveal additional differences on which a taxonomic diagnosis could be based. That eastern and central Brazilian populations of *C. prehensilis* merit such scrutiny is suggested by cytochrome-*b* sequence analyses indicating substantial genetic divergence between them (op. cit.), but it would be prudent to defer formal recognition of any taxa here treated as synonyms of *C. prehensilis* until more comprehensive genetic sampling and morphometric analyses of this widespread species (or species complex) are available.

Specimens examined (N = 98): **Bolivia**—*Beni,* 8 km N Exaltación (AMNH 214613, 214614), near Guayaramerín (AMNH 210337); *La Paz,* Río Madidi (MSB 56078); *Santa Cruz,* Buena Vista (ANSP 14273, FMNH 21396; BMNH 34.9.2.178), 10 km E San Ramón (AMNH 262274), Santa Cruz de la Sierra (BMNH 47.11.22.6 [holotype of *boliviensis*]; 4 km N & 1 km W Santiago de Chiquitos (AMNH 260861). **Brazil**—*Amazonas,*Villa Bella Imperatriz (AMNH 93039, 93040); *Bahia,* Barra (FMNH 21709); *Goiás,* Anápolis (AMNH 134062, 134064, 134066, 134067, 134069–134071); *Mato Grosso,* Chapada dos Guimarães (AMNH 1256/356; ANSP 4802; BMNH 3.7.7.101, 3.7.7.102 [holotype of *centralis*]); *Mato Grosso do Sul,* Maracaju (AMNH 134073); *Minas Gerais,* Lagoa Santa (ZMUC 520–527), Rio Jordão (BMNH 1.11.3.70); *Pará,* 52 km SSW Altamira (USNM 549556), Cametá (AMNH 96315, 96318; MCZ 30556, 30557), Igarapé Assu (BMNH 4.7.4.82), Marajó (USNM 519688); *Roraima,* Boa Vista (FMNH 20031). **Colombia**—*Cesar,* Villanueva (USNM 281897, 281898, 281901–281906, 281908, 281909, 281912, 281914); *Magdalena,* Bonda (AMNH 15459, 15460 [holotype of *sanctaemartae*], 23471–23473); *Meta,* Los Micos (FMNH 87897), Villavicencio (AMNH 73680, 136311). **Ecuador**—*Pastaza,* Río Capihuara (FMNH 43290); *Sucumbíos,* Limoncocha (USNM 528360). **Guyana**—*Rupununi,* 20 mi E Dadanawa (USNM 362242), 30 mi E Dadanawa (ROM 32276), Orinduk (ROM 31420). **Paraguay**—*Concepción,* Yby-Yaú (UMMZ 146507). **Peru**—*Amazonas,* Huampami (MVZ 153571, 153572, 155199, 155201); *Loreto,* Boca Río Curaray (AMNH 72175, 72176), "Mazan River" (AMNH 98579), Nauta (FMNH 122987), Nuevo San Juan (AMNH 268263, 273130), Santa Cecilia (FMNH 86916, 86917), Santa Luisa (FMNH 86915); *Pasco,* Pozuzo (ZMB, uncataloged); *Ucayali,* Balta (LSUMZ 16745). **Surinam**—*Paramaribo,* Paramaribo (FMNH 95783). **Trinidad and Tobago**—*Trinidad,* Caparo (AMNH 24202), Mt. Harris (FMNH 61862, 61863), Princestown (AMNH 4797). **Venezuela**—*Amazonas,* San Juan Manapiare (USNM 406752); *Apure,* Nulita (USNM 442610); *Distrito Federal,* Los Venados (USNM 371277); *Falcón,* Mirimire (USNM 406750); *Monagas,* Caicara (USNM 296617); *Sucre,* Manacal (USNM 406748); *Táchira,* Las Mesas (USNM 443409, 443410); *Zulia,* Cerro Azul (USNM 443408). **Locality unknown** (BMNH 46.8.7.9 [holotype of *tricolor*]).

Coendou pruinosus Thomas, 1905

Coendou pruinosus Thomas, 1905: 310; type locality "Montañas de la Pedregosa," Mérida, Venezuela.
Coendou (*Sphiggurus*) *pruinosus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *vestitus pruinosus*: Cabrera, 1961: 602 (name combination).
Sphiggurus vestitus: Honacki et al., 1982: 572 (name combination, part).
Sphiggurus pruinosus: Woods and Kilpatrick, 2005: 1549 (name combination).

DISTRIBUTION: Examined specimens are from mountains, foothills, and adjacent lowlands (from 54 to 2600 m above sea level) in northeastern Colombia (Meta, Norte de Santander) and northwestern Venezuela (Distrito Federal, Mérida, Zulia).

REMARKS: This species has been considered a subspecies or synonym of *Coendou vestitus* (e.g., by Cabrera, 1961; Honacki et al., 1982), but diagnostic morphological characters of *C. pruinosus* and *C. vestitus* were discussed and illustrated by Voss and da Silva (2001), whose text should be consulted for detailed descriptions, illustrations, and measurements of both species.

SPECIMENS EXAMINED: See Voss and da Silva (2001).

Coendou quichua Thomas, 1899

Coendou quichua Thomas, 1899: 283; type locality "Puembo, Upper Guallabamba River, Province of Pichincha, Ecuador."
Coendou rothschildi Thomas, 1902c: 169; type locality allegedly "Sevilla Island, off Chiriqui, Panama," but this information is fraudulent according to Olson (2008), who claimed that the type was probably collected near Boquerón on the adjacent mainland of Chiriquí province, Panama.
Coendou quichua richardsoni J.A. Allen, 1913: 478; type locality "Esmeraldas (near sea level), Ecuador."
Coendou (*Coendou*) *quichua quichua*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *quichua richardsoni*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *rothschildi*: Tate, 1935: 306 (name combination).
Coendou (*Coendou*) *bicolor quichua*: Cabrera, 1961: 598 (name combination).
Coendou (*Coendou*) *bicolor richardsoni*: Cabrera, 1961: 598 (name combination).

DISTRIBUTION: I have examined specimens of *Coendou quichua* from Panama, western Ecuador (Cotopaxi, Esmeraldas, Pichincha), and trans-Andean Colombia (Cesar, Cundinamarca). Alberico et al. (1999) reported several Colombian specimens (from Chocó and Santander) that I have not seen. Altitudes recorded on specimen labels suggest that the species ranges from sea level to about 3300 m.

REMARKS: *Coendou quichua* was treated as a subspecies of *C. bicolor* by Cabrera (1961), and it is still listed as such by Woods and Kilpatrick (2005). However, it is not clear whether or not Cabrera, Woods, or Kilpatrick ever examined specimens of these strikingly dissimilar taxa. Among other conspicuous differences, *C. quichua* is substantially smaller than *C. bicolor* (tables 4, 8), its longest quills are usually tricolored (all of the quills are normally bicolored in *C. bicolor*), its frontal sinuses are not or only slightly inflated (the frontal sinuses are always inflated in large adults of *C. bicolor*), and the roof of its external auditory meatus usually has a

TABLE 8. Measurements (mm) of Adult Specimens of *Coendou quichua*[a]

	Panama		
	Provincia Chiriquí[b]	Canal Zone[c]	Ecuador[d]
HBL	391 ± 24 (360–420) 10	379 (332–438) 6	367 (345–395) 6
LT	324 ± 41 (270–420) 10	349 (300–413) 6	208 (120–245) 6
HF	69 (67–71) 3	74 (70–78) 6	64 (60–68) 5
CIL	77.5 ± 3.2 (73.2–83.0) 12	78.5 ± 3.9 (73.8–86.9) 10	72.0 (69.2–78.9) 5
LD	22.9 ± 1.7 (19.6–25.6) 12	22.6 ± 2.1 (20.3–27.0) 10	18.9 (15.7–22.2) 7
MTR	17.5 ± 0.6 (16.8–18.5) 12	18.1 ± 0.3 (17.6–18.6) 10	18.0 (17.4–18.5) 7
LM	12.8 ± 0.4 (12.2–13.6) 12	13.2 ± 0.3 (12.6–13.7) 10	13.3 (12.9–13.7) 7
BP4	5.3 ± 0.3 (4.9–5.8) 12	5.4 ± 0.2 (5.0–5.7) 10	5.3 (4.9–5.6) 7
BM1	4.9 ± 0.2 (4.4–5.2) 12	4.9 ± 0.2 (4.6–5.3) 10	4.8 (4.3–5.2) 7
APB	5.0 ± 0.5 (4.2–5.7) 12	5.2 ± 0.7 (4.2–6.5) 10	5.1 (4.2–6.2) 7
PPB	6.8 ± 0.6 (5.7–7.7) 12	7.1 ± 0.6 (6.3–8.4)10	7.4 (6.1–8.5) 6
PZB	44.6 ± 1.0 (43.3–46.3) 10	46.0 ± 2.0 (42.1–48.4) 10	44.3 (42.3–46.2) 5
HIF	11.4 ± 0.8 (10.6–13.3) 12	11.4 ±1.3 (9.7–13.6) 10	10.6 (9.3–12.4) 7
ZL	31.0 ± 1.0 (29.8–33.3) 11	30.6 ± 1.6 (27.2–33.2) 10	29.0 (27.6–30.9) 5
LN	25.2 (22.8–27.6) 2	24.3 (22.5–26.5) 7	24.7 (22.9–27.3) 3
BNA	14.8 ± 1.0 (13.0–16.8) 11	14.3 ± 0.9 (12.5–15.7) 10	11.7 (10.4–12.8) 4
BB	33.7 ± 1.1 (31.5–35.4) 12	34.6 ± 1.1 (32.7–36.4) 10	34.0 (32.6–35.7) 6
DI	4.0 ± 0.3 (3.6–4.4) 12	3.9 ± 0.2 (3.6–4.2) 10	3.9 (3.4–4.3) 7
BIT	5.1 ± 0.4 (4.6–5.8) 10	5.2 ± 0.3 (4.7–5.7) 10	5.4 (5.2–5.6) 4

[a] Tabulated statistics include the sample mean plus or minus one standard deviation (for $N \geq 10$), the observed range (in parentheses), and the sample size.

[b] In western Panama: AMNH 188879–18882, 27066–27069, 27071, 29661; BMNH 3.3.3.93; USNM 248342 (5 males, 6 females, one sex unknown).

[c] In central Panama (now annexed to the provinces of Colón and Panamá): UMMZ 57086; USNM 170953, 171234, 171672, 257360, 266870, 296308, 303277, 303131, 457933 (1 male, 6 females, 3 sex unknown).

[d] From the provinces of Pichincha and Esmeraldas: AMNH 33242 (holotype of *richardsoni*), 46539; BMNH 99.2.18.17 (holotype of *quichua*), 99.2.18.19; NRM A58/2962; ZMUC 2461, 2462 (1 male, 6 sex unknown).

well-developed transverse bony ridge (the roof of the external auditory meatus is always smooth in *C. bicolor*). Although the name *quichua* has traditionally been associated with Ecuadorean material, Panamanian specimens hitherto referred to *rothschildi* are phenotypically similar and appear to be part of a single widespread but geographically variable trans-Andean species.

Thomas (1902c, 1903b) remarked that Panamanian specimens (which he referred to *rothschildi*) are larger than Ecuadorian specimens, are more strongly speckled with white and have more inflated frontal sinuses, wider nasal apertures, and relatively smaller premolars. In fact, Ecuadorean and Panamanian specimens are about equal in size, as indexed by head-and-body length (HBL) or maxillary toothrow length (MTR), but there are some noteworthy morphometric contrasts among representative samples (table 8). In particular, Ecuadorean specimens have much shorter tails (averaging about 55% of HBL) than Panamanian specimens (about 85%–90% of HBL), smaller hind feet, and (as noted by Thomas) much narrower nasal apertures. However, most Ecuadorean specimens are from montane localities (> 2000 m above sea level), whereas most Panamanian specimens are from lowlands and foothills, and this same suite of morphological differences (relative tail length, hind foot size, nasal aperture width)

covaries with elevation in other geographically variable porcupine species (e.g., *C. bicolor* and *C. mexicanus*). The difference in premolar size that Thomas remarked based on the small samples available to him is not apparent in the larger series that I measured.

Most Panamanian specimens of *Coendou quichua* have white-tipped dorsal quills (Reid, 1997: pl. 32, fig. 2), resulting in the boldly speckled effect noted by Thomas, but so few quills are white-tipped on some specimens from central Panama (e.g., MCZ 20576, USNM 170953) that they appear to be almost entirely black, and the only specimens I have seen from eastern Panama (USNM 306980, 335666) have brown-tipped dorsal quills. Most Ecuadorean skins have cream-, buffy-, or brown-tipped dorsal quills, but a few (e.g., EPN 176) are mostly blackish dorsally because only a few pale-tipped quills are scattered along the flanks. Two Colombian specimens (AMNH 73679; LACM 27376) differ from all others referred to this species by having a smooth roof of the external auditory meatus.

Specimens examined (N = 56): **Colombia**—*Cesar,* San Alberto (LACM 27376); *Cundinamarca,* San Juan de Río Seco (AMNH 73679). **Ecuador**—no other locality data (BMNH 34.9.10.185); *Cotopaxi,* Otonga (uncataloged specimen with field number KMH 2218 at USNM); *Esmeraldas,* Esmeraldas (AMNH 33242 [holotype of *richardsoni*]); *Pichincha,* along the Guallabamba river (ZMUC 2462), near Mindo (BMNH 34.9.10.186), below Nono (AMNH 46539, ZMUC 2461), Puembo above the Guallabamba river (BMNH 99.2.18.17 [holotype of *quichua*], 99.2.18.18, 99.2.18.19), Río Saloya (EPN 176), Tablón above Tumbaco (NRM A58/2822, A58/2962, A59/2962), Zámbiza (BMNH 34.9.10.184). **Panama**—*Canal Zone,* no other locality data (FMNH 30742, 30743; USNM 457933), "Atlantic Side" (MCZ 21515B, 21516), Barro Colorado Island (USNM 257360, 521066), Camp Piña (USNM 303131), Cativá Road (USNM 303277), Chagres River (USNM 266870), Fort Davis (USNM 298915), Fort Kobbe (USNM 296308), Fort Sherman (MCZ 21515A, 27460), France Field (MCZ 20576, 20577), Frijoles (UMMZ 57086), Gatun (USNM 171234, 171672), Río Indio (USNM 170953); *Chiriquí,* Bogava (BMNH 3.3.3.93, USNM 248342), Boquerón (AMNH 18879–18882, 27067–27071, 29661; FMNH 14181, 14182), Boquete (AMNH 27066), "Sevilla Island" (BMNH 3.3.1.93 [holotype of *rothschildi*]); *Darién,* Boca Río Paya (USNM 306980); *Herrera,* Parita (USNM 283123); *San Blas,* Armila (USNM 335666).

Coendou roosmalenorum Voss and da Silva, 2001

Coendou roosmalenorum Voss and da Silva, 2001: 24; type locality "Novo Jerusalem near the left bank of the middle Rio Madeira in the Brazilian state of Amazonas."

Sphiggurus roosmalenorum: Woods and Kilpatrick, 2005: 1549 (name combination).

Distribution: *Coendou roosmalenorum* occurs on both banks of the Rio Madeira in the Brazilian states of Amazonas and Rondônia. Although specimens have only been collected at three localities (Voss and da Silva, 2001), photographs of a small porcupine closely resembling this species were taken in 1992 on the south bank of the Amazon near Alvarães (13°13′S, 64°48′W), about 500 km NW of the type locality (Franz Kern, personal commun., 2011).

REMARKS: This species may be closely related to *Coendou ichillus, C. pruinosus,* and *C. vestitus,* all of which also have bristle-quills in addition to ordinary defensive quills and soft fur in their dorsal pelage. Diagnostic comparisons with those species were provided by Voss and da Silva (2001), whose text should also be consulted for a detailed description of the skin and skull of *C. roosmalenorum.*

SPECIMENS EXAMINED: See Voss and da Silva (2001).

Coendou rufescens (Gray, 1865)

Erethizon (*Echinoprocta*) *rufescens* Gray, 1865: 321; type locality "Columbia" (= Colombia).
Coendou prehensilis rufescens: Trouessart, 1897: 621 (name combination).
Echinoprocta rufescens: Cabrera, 1901: 159 (name combination).
Coendou sneiderni Lönnberg, 1937: 17; type locality "Munchique, Cauca" in the Cordillera Occidental (western Andes) of Colombia.
Coendou rufescens: Alberico et al., 1999: 606 (name combination).

DISTRIBUTION: Based on examined specimens and credible literature records, *Coendou rufescens* occurs in all three Andean cordilleras of Colombia (Alberico et al., 1999), on both slopes of the Ecuadorean Andes, in northern Peru (Lambayeque; Pacheco et al., 2009), and in northern Bolivia (Cochabamba; see Remarks, below). Elevations recorded on specimen tags and in the literature document an elevational range from about 800 to 3500 m above sea level, but most records are clustered in the interval from 1500 to 3000 m (Trouessart, 1920; Lönnberg, 1937; Alberico et al., 1999; Orcés and Albuja, 2004; this report).

REMARKS: This species has long been referred to the monotypic genus *Echinoprocta,* but there is no compelling evidence that *rufescens* is anything other than a short-tailed species of *Coendou.* Because the retention of *Echinoprocta* as a distinct genus (e.g., by Woods and Kilpatrick, 2005) does not appear to be motivated by any defensible hypothesis of reciprocal monophyly, I follow Alberico et al. (1999) in treating it as a subjective junior synonym of *Coendou.* Subsequent to Gray's (1865) original description, this species was redescribed by Cabrera (1901), Trouessart (1920), Lönnberg (1937), and Alberico et al. (1999). As noted by Alberico et al. (1999), most specimens have a naked, calloused patch of skin on the dorsal surface of the tip of the tail, suggesting that this organ is prehensile like those of other Neotropical porcupines (contra Ellerman, 1940).

The holotype of *Coendou rufescens* (BMNH 53.9.28.30) is a young adult with newly erupted P4 and unfused cranial sutures. The skin is in excellent condition, but the skull (evidently extracted from the mounted skin sometime after Gray's description) is fragmentary: the dentition is complete, but the occiput and most of the basicranium is missing, as is the right zygoma, most of the left zygoma, both nasals, and most of the premaxillae. In fact, the only taxonomically useful measurement that can be taken is length of the maxillary tooth row (MTR), which is 15.6 mm. By comparison, the maxillary tooth rows of nine adult specimens collected in the Cordillera Occidental (western Andes) of Colombia range from 16.7 to 19.2 mm, whereas the

TABLE 9. Measurements (mm) of Adult Specimens of *Coendou rufescens*

	Colombia			Ecuador	Bolivia
	AMNH 73678♂[a]	USNM 236908[a,b]	Cordillera Occidental[c]	MCZ 36327♂	CM 5255♀
HBL	ca. 365	—	368 (340–410) 10	350	360
LT	ca. 150	—	139 (120–175) 10	119	140
HF	—	—	67 (62–72) 6	—	61
CIL	72.4	66.0	73.1 (67.1–78.0) 9	73.3	65.9
LD	18.8	16.5	19.5 (16.9–21.6) 9	20.3	16.3
MTR	16.7	17.4	17.7 (16.7–19.2) 9	17.4	17.3
LM	12.0	12.9	12.8 (11.8–14.2) 9	12.7	12.7
BP4	4.9	5.6	5.3 (5.1–5.6) 9	5.2	5.0
BM1	4.2	4.4	4.7 (4.4–5.1) 9	4.4	4.5
APB	3.5	3.8	4.8 (4.1–5.7) 9	5.3	4.8
PPB	5.3	6.2	7.3 (6.1–8.8) 8	7.8	7.1
PZB	44.0	39.5	43.8 (41.8–45.2) 9	44.4	—
HIF	10.6	10.1	10.8 (9.9–12.2) 10	12.8	9.5
ZL	27.0	26.2	29.1 (27.5–31.2) 10	29.1	27.1
LN	23.4	21.0	24.1 (22.5–27.2) 6	24.2	—
BNA	11.4	10.8	11.9 (10.6–12.9) 10	10.9	—
BB	30.1	29.9	30.6 (28.8–33.1) 9	30.7	31.6
DI	3.0	3.1	3.6 (3.2–3.7) 10	4.0	3.2
BIT	4.6	4.4	5.2 (4.7–5.7) 9	5.0	5.2

[a] From the Cordillera Oriental (eastern Andes).
[b] Sex unknown.
[c] Western Andes. Table entries include the mean, observed range (in parentheses), and sample size for measurements of the following series: AMNH 181483, 181484; FMNH 86765, 88524, 88526, 89262–89266 (2 males, 8 females).

same dimension in two adults from the Cordillera Oriental (eastern Andes) of Ecuador are 16.7 and 17.4 mm. Thus, the tooth row of the type is shorter than those of other specimens that I refer to *C. rufescens*. Alberico et al. (1999) plausibly suggested that the type was collected somewhere in the Cordillera Oriental of Colombia, from which additional material should be examined for any future revisionary study.[5]

The single Bolivian specimen I examined (CM 5255) is morphologically indistinguishable from Colombian and Ecuadorian material that I directly compared with it. The specimen is a very young adult (with newly erupted and almost unworn P4), which plausibly explains its small values for some age-dependent dimensions (e.g., CIL and LD; table 9). I am, frankly, at a loss to explain how this species could be distributed over thousands of kilometers of highly dissected terrain with negligible geographic variation. Perhaps it is not fanciful to think that the Inca, who transplanted whole human populations from one end of the Andes to the other, might also have transported captive stock of this strikingly beautiful rodent over equivalent distances.

Woods and Kilpatrick (2005) listed *epixanthus* Martínez (1873) as a synonym of this species, but Martínez simply applied the name *epixanthus* Brandt, 1835—a synonym of *Erethizon*

[5] Although these authors "restricted" the type locality of *Coendou rufescens* to "Quebrada Susumuco, 13 km WNW Villavicencio" in the Colombian department of Cundinamarca (Alberico et al., 1999: 607), there appears to be no evidence that the type was actually collected there.

dorsatum—to a Colombian specimen of *Coendou rufescens*. Therefore, his usage represents a misidentification, not a new name.

Specimens examined ($N = 25$): **Bolivia**—*Cochabamba,* Incachaca (CM 5255). **Colombia**—No other locality data (BMNH 53.9.28.30 [holotype of *rufescens*]); *Cauca,* Charguayaco (FMNH 88525, 89262), La Vega (FMNH 86765), Munchique (FMNH 88524, 89261, 89264, 89265), Paispamba (ROM 57254), Quintana (AMNH 181483, 181484; FMNH 88526, 88527, 89263), Sabanetas (FMNH 89266); *Cundinamarca,* Chingasa (MNHN1936-1932), Fómeque (AMNH 150028, USNM 236908), La Aguadita (AMNH 73678); *Valle del Cauca,* 4 km NW San Antonio (MVZ 124088). **Ecuador**—*Azuay,* Valle de Yunguilla (QCAZ 7591); *Tungurahua,* Baños (MCZ 36327, UMMZ 83268), Tambo Jaramillo (FMNH 47054).

Coendou spinosus (F. Cuvier, 1823)

Hystrix couiy Desmarest, 1822: 345 (part); type locality "Le Mexique et sans doute le Brésil; le Paraguay."
Sphiggure spinosa F. Cuvier, 1823: 433; type locality Sapucaí, Paraguarí, Paraguay (fixed by neotype selection; see Remarks, below).
Sphiggure villosa F. Cuvier, 1823: 434; type locality unknown (see Remarks, below).
Cercolabes (*Sphiggurus*) *nigricans* Brandt, 1835: 403; type locality "Brasilia" (= Brazil).
Cercolabes (*Sphiggurus*) *affinis* Brandt, 1835: 412; type locality "Brasilia" (= Brazil).
Sphingurus sericeus Cope, 1889: 136; type locality São João do Monte Negro (= Montenegro; Paynter and Traylor, 1991), Rio Grande do Sul, Brazil (Koopman, 1976).
Synetheres (*Synetheres*) *spinosus*: Trouessart, 1881: 183 (name combination).
Synetheres (*Sphiggurus*) *villosus*: Trouessart, 1881: 184 (name combination).
Coendu affinis: Trouessart, 1897: 623 (name combination).
Coendu spinosus: Trouessart, 1897: 622 (name combination).
Coendu sericeus: Trouessart, 1897: 623 (name combination).
Coendu villosus: Trouessart, 1897: 622 (name combination).
Coendou roberti Thomas, 1902d: 63; type locality Roça Nova, Serra do Mar, Paraná, Brazil.
Coendou (*Sphiggurus*) *spinosus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *villosus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *nigricans*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *affinis*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *sericeus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *roberti*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *spinsosus nigricans*: Cabrera, 1961: 601 (name combination).
Coendou (*Sphiggurus*) *spinosus roberti*: Cabrera, 1961: 602 (name combination).
Coendou (*Sphiggurus*) *spinosus spinosus*: Cabrera, 1961: 602 (name combination).

Distribution: *Coendou spinosus* occurs in humid tropical and subtropical forests of the Mata Atlântica of southeastern Brazil (from Espírito Santo southward to Rio Grande do Sul) and in the contiguous subtropical forests of northern Uruguay (Artigas, Rivera, Salto, Tacuarembó; Ximénez et al., 1972), northeastern Argentina (Misiones; Crespo, 1974), and eastern Paraguay. Examined specimens document an altitudinal range from near sea level to at least 900 m.

TABLE 10. Measurements (mm) of Adult Specimens of *Coendou spinosus*[a]

		Brazil	
	Paraguay[b]	Paraná & Santa Catarina[c]	Rio de Janeiro & São Paulo[d]
HBL	317 (288–340) 8	393 (330–470) 9	339 (315–390) 6
LT	255 (230–285) 8	282 (240–330) 9	275 (245–296) 6
HF	64 (60–67) 7	67 (63–76) 9	67 (62–70) 6
CIL	62.9 (59.9–67.3) 8	68.6 (65.9–76.1) 5	69.8 (65.4–74.0) 5
LD	15.2 (14.0–16.7) 8	17.6 (15.5–19.9) 7	18.4 (16.0–21.4) 7
MTR	15.6 (15.2–16.1) 8	16.3 (15.3–17.0) 8	15.9 (15.1–16.9) 7
LM	11.5 (11.1–11.9) 8	11.9 (11.2–12.4) 8	11.6 (10.9–12.3) 7
BP4	4.5 (4.3–4.8) 8	4.6 (4.4–5.0) 8	4.5 (4.2–4.7) 7
BM1	4.3 (4.0–4.6) 8	4.4 (4.0–4.8) 8	4.2 (4.0–4.5) 7
APB	5.1 (4.3–5.6) 8	5.2 (4.7–5.8) 8	5.0 (4.2–5.5) 7
PPB	7.3 (6.3–8.0) 8	7.9 (6.6–8.7) 7	7.4 (7.0–8.2) 7
PZB	42.5 (41.2–45.1) 5	44.3 (41.9–46.6) 6	43.8 (40.3–45.2) 4
HIF	8.5 (7.2–9.7) 8	8.9 (7.4–10.2) 8	9.6 (8.4–10.4) 7
ZL	27.5 (25.1–29.2) 8	29.0 (27.2–30.7) 7	29.0 (27.8–29.8) 6
LN	20.5 (17.4–22.7) 7	22.0 (19.6–25.8) 6	22.5 (20.6–24.2) 5
BNA	9.7 (8.4–10.9) 8	10.8 (9.8–12.1) 4	11.6 (9.8–13.3) 7
BB	31.2 (29.7–32.7) 8	33.0 (31.9–35.0) 6	31.9 (30.5–33.4) 4
DI	3.2 (2.9–3.6) 8	3.6 (3.2–4.0) 7	3.5 (3.2–3.7) 7
BIT	4.4 (3.7–5.0) 8	4.9 (4.4–5.5) 7	4.8 (4.3–5.3) 7

[a] Table entries include the mean, observed range (in parentheses), and sample size for each measurement.

[b] BMNH 2.4.7.28, 2.4.7.29, 25.5.1.10; MSB 54078; UMMZ 68132; USNM 115122, 115123; ZMB 35756 (2 males, 5 females, 1 sex unknown).

[c] BMNH 3.7.1.98a, 3.7.1.99, 3.7.1.100, 3.7.1.102, 14.5.9.17, 14.5.9.18, 29.6.6.67–29.6.6.69 (3 males, 5 females, 1 sex unknown).

[d] BMNH 92.11.24.1, 92.11.24.2, 98.1.6.1, 2.11.8.14; MCZ 1832; USNM 259793, 259838 (2 males, 2 females, 3 sex unknown).

REMARKS: The specimens I refer to *Coendou spinosus* are small to medium-size porcupines (table 10) with long (55–80 mm) tricolored quills intermingled with shorter bicolored quills over most of the dorsal surface. Most specimens have long fur, the individual hairs of which are blackish basally but have pale (grayish, yellowish, or orange) tips; in some specimens the fur is long enough to conceal the underlying quills over much of the body, but in other specimens the fur is sparser and lies over the quills in scattered tufts, and a few skins completely lack long fur (appearing entirely spiny; see below). The ventral pelage consists entirely of soft fur. The mystacial vibrissae and the stiff bristles on the underside of the tail are usually bicolored: blackish basally with yellowish or orange tips. The frontal sinuses are not inflated and the dorsal roof of the external auditory meatus is smooth (without a bony dorsal ridge or keel). By comparison, *Coendou insidiosus* (a geographically adjacent small species of long-furred Brazilian porcupine) differs from *C. spinosus* by having only short (≤ 35 mm) bicolored quills; pale-based or completely pale fur (whitish in some specimens); unicolored (brownish or blackish) mystacial vibrissae and caudal bristles; and shorter tooth rows (MTR < 14.5 mm; Voss and Angermann, 1997). *Coendou nycthemera,* another small species that occurs in eastern Brazil, differs from *C. spinosus* by consistently lacking long dorsal fur, by having spiny

ventral pelage, by having unicolored mystacial vibrissae and caudal bristles, and perhaps in other diagnostic traits described by Handley and Pine (1992) but not carefully evaluated for this report.

Geographic variation among examined specimens that I refer to this species includes modest size differences between Paraguayan and Brazilian samples (perhaps exaggerated by the prevalence of young adults in the Paraguayan material; table 10) and the more saturated pigments of specimens from more northern localities by comparison with those from southern localities. Whereas skins from Rio de Janeiro and São Paulo usually have orange-tipped tricolored quills and orange-highlighted fur, specimens from Rio Grande do Sul and Paraguay usually have yellow-tipped tricolored quills and fur that is washed with pale yellow dorsally and pale gray ventrally. Because geographically intermediate specimens (from Paraná and Santa Catarina) seem intermediate in pelage characters, this pigmental variation could plausibly be interpreted as clinal. One specimen from Espírito Santo (BMNH 3.9.4.87, discussed by Voss and Angermann, 1997: 33) has pale-gray fur, superficially resembling that of *Coendou insidiosus*.

This species was first described by Azara (1801), who used the vernacular name "couiy" for a small Paraguayan porcupine with tricolored quills mixed with long fur. Azara's description served as the basis for *paragayensis* Oken, 1816, but Oken's names are technically unavailable (Hershkovitz, 1949; ICZN, 1956). Another epithet based (in part) on Azara's porcupine is *couiy* Desmarest, 1822, but this is a nomen oblitum that does not appear to have ever been used by 20th-century authors as a valid name; under Article 23.9 of the current code (ICZN, 1999), it cannot replace *spinosus* F. Cuvier, 1823, which is the name now commonly used for the small Paraguayan species (e.g., by Cabrera, 1961; Woods, 1993; Woods and Kilpatrick, 2005; D'Elía et al., 2008).

Frédéric Cuvier's important essay on porcupine taxonomy, "*Examen des espèces du genre porc-épic . . .*" bears the typographic date of 1822, but according to Sherborn (1914) it was not issued until November of 1823. Although Cuvier said that the species he called *Sphiggure spinosa* appeared to be the same as the one described by Azara, Cuvier obviously had a specimen in front of him, because many of the external characters he described were not mentioned by Azara. Waterhouse (1848) examined a specimen in Paris that he believed to be Cuvier's type, but this specimen was apparently lost or discarded sometime in the following decades. It was not listed among the extant rodent types in the Paris museum by Rode (1945), and a careful search of the MNHN collections by L. Granjon (personal commun., 1997) did not turn up any material that could be positively identified as such.

Cuvier did not say where the type of *spinosus* was collected, but his description and measurements are consistent with current usage of this name for the small porcupine that occurs in eastern Paraguay and southeastern Brazil. The only noteworthy discrepancy concerns the occurrence of long fur, which was said to be absent from the type (Cuvier, 1823; Waterhouse, 1848). Most specimens from Paraguay and SE Brazil have long fur (partially or completely concealing the spines), but a few skins from throughout the range of this species do not (e.g., BMNH 28.10.11.47 from Santa Catarina; BMNH 3.7.1.97 from Paraná; BMNH 92.11.24.1 from Rio de Janeiro), so this trait appears to be subject to individual (or seasonal) variation.

The taxonomic application of *spinosus* is therefore ambiguous due to the absence of a type, lack of a definite type locality, and controversy regarding the taxonomic significance of long fur (see below). In order to fix the current application of this name for the small porcupine of eastern Paraguay (which might eventually prove to be taxonomically distinct from nominal taxa occurring in Brazil), I hereby select as the neotype of *Coendou spinosus* a specimen in the National Museum of Natural History (USNM 115122) consisting of the skin and skull of a young adult male collected by William Foster at Sapucay (= Sapucaí at 25°40′S, 57°38′W; Paynter, 1989) in the Paraguayan department of Paraguarí.

Also named by F. Cuvier in the same publication as *Sphiggure spinosa* was *S. villosa,* a Brazilian porcupine said to differ from the former by having long fur. Although some authors (e.g., Waterhouse, 1848; Emmons and Feer, 1997) have treated *spinosus* and *villosus* as valid species, others have regarded these names as synonyms based on individual or seasonal differences in fur length (e.g., I. Geoffroy St.-Hilaire, 1828; Handley and Pine, 1992). Unhappily, the type of *villosus* is also lost. The specimen that Rode (1945) erroneously identified as the type of *villosus* was among the material examined by F. Cuvier, and it is still in the Paris museum; however, this specimen lacks long fur and was collected by Delaland (L. Granjon, personal commun., 1997), whereas the type of *villosus* was a long-furred animal collected by Auguste de Saint-Hilaire (Cuvier, 1823). Woods and Kilpatrick (2005) gave the type locality of *villosus* as "Brazil, mountains near Rio de Janeiro, Corcoracto," which corresponds to the geographic information accompanying Delaland's specimen (Rode, 1945). In effect, the type locality of *villosus* is unknown.

In the event that future research shows that one or more Brazilian populations merit recognition as distinct taxa, a neotype should perhaps be designated to fix the application of *villosus,* the oldest and most widely used of the several epithets herein treated as junior synonyms of *Coendou spinosus.* Although the types of *affinis* and *nigricans* are extant, they consist of mounted skins only (without accompanying skulls; contra Abramov and Baranova, 2008) in the Russian Academy of Sciences in St. Petersburg. Because their type localities are indefinite, the taxonomic application of these names is likely to remain problematic. Two other names, *sericeus* and *roberti,* are based on type specimens from well-documented type localities, but neither has been widely used for eastern Brazilian porcupines.

Specimens examined (N = 54): **Argentina**—*Misiones,* Jardín América (OMNH 36902). **Brazil**—no other locality data (ZINRAS 30 [holotype of *nigricans*], 31 [holotype of *affinis*]); *Espírito Santo,* Engenheiro Reeve (BMNH 3.9.4.87); *Minas Gerais,* Lagoa Santa (ZMUC 501, 502, 504–511, 514, 515); *Paraná,* Roça Nova (BMNH 3.7.1.97 [holotype of *roberti*], 3.7.1.98–3.7.1.102); *Rio de Janeiro,* Nova Friburgo (USNM 259793, 259838), Porto Real (BMNH 92.11.24.1, 92.11.24.2), "Rio 125 m" (BMNH 98.1.6.1), Santa Rita do Rio Negro (MCZ 1832), 5 mi N Terezópolis (FMNH 26571); *Rio Grande do Sul,* São João do Monte Negro (ANSP 4804 [holotype of *sericeus*]), Taquara do Mundo Novo (ZINRAS 2789, 2790, 2792, 6595); *Santa Catarina,* Colônia Hansa (BMNH 28.10.11.48, 29.6.6.67–29.6.6.69; ZMB 42567), Humboldt (BMNH 14.5.9.17, 14.5.9.18); *São Paulo,* Butantan (ZMB 35529), São Sebastião (BMNH 2.11.8.14). **Paraguay**—*Caazapá,* Estancia Dos Marías (UMMZ 174975); *Concepción,* Horqueta

(UMMZ 68132); *Guaira,* Villarica (BMNH 25.5.1.10; ZMB 40471); *Itapúa,* El Tirol (MSB 54078), Estancia San Isidro (GD 252 [field number of uncataloged specimen at UMMZ]); *Paraguarí,* Sapucay (BMNH 2.4.7.28, 2.4.7.29; USNM 115122 [neotype of *spinosus*], 115123); *San Pedro,* Molinasque (ZMB 35756).

Coendou vestitus Thomas, 1899

Coendou vestitus Thomas, 1899: 284 (original description).
Coendou (*Sphiggurus*) *vestitus*: Tate, 1935: 307 (name combination).
Coendou (*Sphiggurus*) *vestitus vestitus*: Cabrera, 1961: 603 (name combination).
Sphiggurus vestitus: Honacki et al., 1982: 572 (name combination).

DISTRIBUTION: I have examined specimens of *Coendou vestitus* from only two definitely identifiable localities, both of which are in the western foothills of the eastern Andean cordillera in the Colombian department of Cundinamarca. However, Alberico et al. (1999) report a specimen from Villavicencio, on the eastern side of the Andes in the department of Meta.

REMARKS: This species may be closely related to *Coendou ichillus, C. pruinosus,* and *C. roosmalenorum,* all of which also have bristle-quills in addition to ordinary defensive quills and soft fur in their dorsal pelage (Voss and da Silva, 2001). Diagnostic comparisons with those species were provided by Voss and da Silva (2001), whose text should also be consulted for a detailed description of the skin and skull of *C. vestitus.*

SPECIMENS EXAMINED: See Voss and da Silva (2001).

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